



The Pinnotheridae of the northeastern Pacific (Alaska to Mexico): zoogeographical remarks and new bivalve hosts (Crustacea, Brachyura, Pinnotheridae)

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Abstract

New bivalve host records for four pinnotherid crabs of the Mexican Pacific are reported: *Fabia subquadrata* Dana, 1851, in *Modiolus capax* (Conrad, 1837); *Opisthopus transversus* Rathbun, 1893, in *Tivela stultorum* (Mawe, 1823); *Pinnaxodes gigas* (Green, 1992), in *Pinna rugosa* (Sowerby, 1835), and *Panopea generosa* Gould, 1850; and *Tumidotheres margarita* (Smith, 1870), in *Nodipecten subnodosus* (Sowerby, 1835). The southernmost distribution of *F. subquadrata* is extended to about 600 km along the west coast of the Baja California Peninsula; the distribution of *P. gigas* is extended outside the Gulf of California more than 1000 km north to San Quintín, on the west coast of Baja California; and the range of *T. margarita* is restricted on the west coast of Baja California to Scammon's Lagoon, Baja California Sur and Playa Kino Viejo, Sonora in the central region of the Gulf of California, Mexico to Panama. Based on the new material, new information on taxonomy, ecology, and life history is provided for each of these species. *Pinnotheres nudus* Holmes, 1895 is restored as a valid species and is removed from its synonymy with *O. transversus*. An updated checklist with remarks on zoogeography for the 60 pinnotherid species, included in 23 genera, of the northeastern Pacific region (Alaska to the Mexican tropical Pacific) is given.

Key words: Baja California Peninsula, Mollusca, Pelecypoda, taxonomy

Resumen

Se presentan nuevos huéspedes bivalvos para cuatro especies de cangrejos pinotéridos del Pacífico mexicano: *Fabia subquadrata* Dana, 1851, en *Modiolus capax* (Conrad, 1837); *Opisthopus transversus* Rathbun, 1893, en *Tivela stultorum* (Mawe, 1823); *Pinnaxodes gigas* (Green, 1992), en *Pinna rugosa* (Sowerby, 1835), y *Panopea generosa* Gould, 1850; y *Tumidotheres margarita* (Smith, 1870), en *Nodipecten subnodosus* (Sowerby, 1835). La distribución de *F. subquadrata* se extendió cerca de 600 km más al sur a lo largo de la costa oeste de la península de Baja California; el límite norteño de *P. gigas* se extiende fuera del Golfo de California a más de 1000 km hasta San Quintín en la costa oeste de Baja California; y *T. margarita* se restringe sobre la costa oeste de Baja California a la Laguna Ojo de Liebre, Baja California Sur y a Playa Kino Viejo, Sonora en la región central del Golfo de California, México hasta Panamá. Con base en el nuevo material algunas observaciones sobre taxonomía, ecología, y ciclo de vida se discuten para estas especies. *Pinnotheres nudus* Holmes, 1895, es restablecida como una especie válida y es removida de la sinonimia de *O. transversus*. Se presenta una lista actualizada de las 60 especies de los pinotéridos, incluidos en 23 géneros, del Pacífico noreste (de Alaska hasta el Pacífico mexicano) con su distribución y algunos comentarios sobre su zoogeografía.

Palabras clave: Península de Baja California, Mollusca, Pelecypoda, taxonomía

Introduction

The Pinnotheridae de Haan, 1833 comprises a group of symbiotic crabs living in association with Chordata (Ascidacea), Crustacea (Thalassinidea), Echinodermata (Echinoidea and Holothurioidea), Mollusca (Bivalvia and Gastropoda), Polychaeta, and less frequently with Brachiopoda, Echiura, and Sipuncula (Schmitt *et al.* 1973; Anker *et al.* 2005; Castro 2015; Palacios-Theil, 2016). Sixty species of these symbiotic crabs in 23 genera have

been recorded for the northeastern Pacific coast (Alaska to Mexican Tropical Pacific; Table 1), *Pinnixa* being the most diverse genus in the region with 24 described species (Glassell 1935b; Hendrickx 1995; Campos 1996, 2002, 2004, 2009; Campos & Wicksten 1997; Campos *et al.* 1992, 1995, 1998, 2009, 2012; Campos & Vargas-Castillo 2013; Salgado 2015). Recent examination of a large pen shell, *Pinna rugosa* (Sowerby, 1835), from the Gulf of California and several specimens of horse mussel (*Modiolus capax* Conrad, 1837), Pismo clam (*Tivela stultorum* (Mawe, 1823)), giant lion's paw scallop (*Nodipecten subnudosus* (Sowerby, 1835)), and geoduck (*Panopea generosa* Gould, 1850), from the west coast of Baja California Peninsula resulted in four pinnotherid species recorded for the first time in symbiosis with these bivalves. Furthermore, the distribution of *Tumidotheres margarita* (Smith, 1870) is revised and some females identified as *T. margarita* by Campos (1989b) were found not to belong in this species. The morphology of *Pinnotheres nudus* Holmes, 1895 is also reassessed. An updated distributional checklist of the pinnotherid crabs of the northeastern Pacific region is presented with some zoogeographical remarks.

TABLE 1. Pinnotheridae of the northeastern Pacific coast, from Alaska, U.S.A. to Mexico.

***Alarconia* Glassell, 1938**

1. *Alarconia seaholmi* Glassell, 1938

Distribution. Acapulco, Guerrero, Mexico (type locality) (Glassell 1938).

***Austinixa* Heard & Manning, 1997**

2. *Austinixa felipensis* (Glassell, 1935)

Distribution. San Felipe, Baja California, (Gulf of California), Mexico (type locality); Corral de Mulas and La Cepona, El Salvador; Enramada, Panama (Manning & Felder 1989; Palacios-Theil *et al.* 2016).

***Austinothere* Campos, 2002**

3. *Austinothere angelicus* (Lockington, 1877)

Distribution. San Felipe and Los Angeles Bay (type locality), Baja California, (Gulf of California), Mexico; Costa Rica; Colombia (Lemaitre & Álvarez-León 1992; Campos 2002; Campos & Vargas-Castillo 2014).

***Bonita* Campos, 2009**

4. *Bonita mexicana* Campos, 2009

Distribution. Point Sofia, Tortugas Bay, Baja California Sur, Mexico (type locality) (Campos 2009).

***Calyptraeotheres* Campos, 1990**

5. *Calyptraeotheres camposi* Ayón-Parente & Hendrickx, 2014

Distribution. Off El Huizache, off Altata (type locality), off Río Baluarte, and off Teacapan, Sinaloa, (SE Gulf of California), Mexico (Ayón-Parente & Hendrickx 2014).

6. *Calyptraeotheres granti* (Glassell 1933)

Distribution. Throughout the Gulf of California and Magdalena Bay (type locality) on the west coast of Baja California Sur, Mexico (Glassell 1933, 1935a; Hernandez-Avila & Campos 2006).

7. *Calyptraeotheres pepeluasi* Campos & Hernández-Ávila, 2010

Distribution. off Lázaro Cardenas port, Michoacán, Pacific coast of Mexico (type locality) (Campos & Hernández-Ávila 2010).

***Clypeasterophilus* Campos & Griffith, 1990**

8. *Clypeasterophilus ususfructus* (Griffith, 1987)

Distribution. Off Cabo San Miguel, Baja California, Mexico; SSE of Judas Point, Costa Rica (Zaca Expedition, station 214; type locality); SW of Secas Is., Panama; off Santa Elena Bay, Ecuador (Griffith 1987; Hendrickx 1990).

***Dissodactylus* Smith, 1870**

9. *Dissodactylus glasselli* Rioja, 1944

Distribution. San Benito beach, near Tapachula, Chiapas, Mexico (type locality; Rioja, 1944); El Triunfo port, El Salvador; Parque Nacional Manuel Antonio, Quepos, Puntarenas, Costa Rica (Griffith 1987; Pohle & Marques 1995).

10. *Dissodactylus lockingtoni* Glassell, 1935

Distribution. Campo Don Abel, about 24 km north San Felipe, Baja California and Puerto Peñasco, Sonora, (northern Gulf of California), Mexico; San Benito (= Puerto Chiapas), Chiapas, about 50 km from Tapachula, Mexico (type locality); Puntarenas beach, Puntarenas, Costa Rica (Pohle & Marques 1995; present study).

11. *Dissodactylus nitidus* Smith, 1870

Distribution. San Felipe, Baja California, Puerto Peñasco, Sonora, and Concepcion Bay, Baja California Sur, (Gulf of California), Mexico; Abreojos Point and Santa Maria Bay on the west coast of Baja California Sur, Mexico; Puerto el Triunfo, El Salvador (type locality); Sechura Bay, Peru (Griffith 1987; present study)..

12. *Dissodactylus schmitti* Griffith, 1987

Distribution. Five miles north of White Friars (= Los Morros de Potosí, Los Frailes Blancos), Zihuatanejo, Guerrero, Mexico, 17°31'N, 101°29'W, (type locality) (Griffith 1987).

13. *Dissodactylus xantusi* Glassell, 1936

Distribution. San Felipe and Espiritu Santo Island (type locality), Baja California and Puerto Peñasco, Sonora, (Gulf of California), Mexico, to Venado Beach, Panama (Griffith 1987).

***Enigmatheres* Campos, 2002**

14. *Enigmatheres canfieldi* Rathbun, 1917

Distribution. Monterey, California, U.S.A. (type locality) (Campos 2009).

***Fabia* Dana, 1851**

15. *Fabia carvachoi* Campos, 1996

Distribution. Campo El Pescador, near San Felipe, Baja California, (northern Gulf of California), Mexico (type locality) (Campos 1996).

16. *Fabia concharum* (Rathbun, 1893)

Distribution. San Pedro and San Diego Bay (type locality), California, U.S.A. to Magdalena Bay, Baja California Sur, Mexico. (Campos 1996).

17. *Fabia subquadrata* Dana, 1851

Distribution. Akutan Pass, Alaska, U.S.A.; “in freto ‘Puget’ Oregoniae”= Puget Sound, Washington, U.S.A. (type locality) to El Coyote Estuary, Punta Abreojos, Baja California Sur, Mexico (Campos 1996; present study).

***Glassella* Campos & Wicksten, 1997**

18. *Glassella costaricana* (Wicksten, 1997)

Distribution. Manzanillo beach, Acapulco, Guerrero, Mexico and Playa del Coco, Guanacaste, Costa Rica (type locality) (Campos & Wicksten 1997; Campos *et al.* 1998).

***Holothuriophilus* Nauck, 1880**

19. *Holothuriophilus traspeziformis* (Nauck, 1880)

Distribution. Mazatlán, Sinaloa (type locality) and Ixtapa, Zihuatanejo Bay, Guerrero, Mexico (Campos *et al.* 2012).

***Juxtafabia* Campos, 1993**

20. *Juxtafabia muliniarum* Rathbun, 1918

Distribution. Lower [= Baja] California (type locality) and Gulf of Santa Clara, Sonora, (northern Gulf of California), Mexico to Costa Rica (Green 1985; Campos 1993).

***Opisthopus* Rathbun, 1893**

21. *Opisthopus transversus* Rathbun, 1893

Distribution. Santa Cruz and Monterey (type locality), California, U.S.A. to San Ignacio Lagoon, Baja California Sur, Mexico (Campos & Manning 2000; this paper).

***Parapinnixa* Holmes, 1895**

22. *Parapinnixa affinis* Holmes, 1900

Distribution. Dead Man's Is., San Pedro, California, U.S.A., (type locality) to La Bajada, Tortugas Bay, Baja California Sur, Mexico (Campos *et al.* 1992).

23. *Parapinnixa nitida* (Lockington, 1877)

Distribution. Magdalena Bay, west coast of Baja California Sur and from San Felipe and Los Angeles Bay, Baja California (type locality), to La Paz, Baja California Sur, (Gulf of California), Mexico (Schmitt *et al.* 1973).

***Pinnixa* White, 1846**

24. *Pinnixa abbotti* Glassell, 1935

Distribution. San Felipe (type locality) and Los Angeles Bay, Baja California, (Gulf of California), Mexico (Glassell 1935b; Palacios-Theil *et al.* 2016).

25. *Pinnixa affinis* Rathbun, 1898

Distribution. Bay of Panama, 8°27'60"N, 7°935'00"W (type locality); Newport Bay, California, U.S.A., (probably extralimital, needs confirmation) (Glassell 1934). Glassell (1934) speculated on the presence of this species in the Gulf of California; record from Mazatlán Bay, Sinaloa, Mexico by Hendrickx (1995) needs confirmation since the studied material has apparently been lost.

26. *Pinnixa barnharti* Rathbun, 1918

Distribution. Puget Sound, Washington and under pier at Venice, California U.S.A. (type locality), to Punta Banda estuary, Todos Santos Bay, Ensenada, Baja California, Mexico (Zmarzly 1992; Campos *et al.* 1998).

27. *Pinnixa eburna* H. W. Wells, 1928

Distribution. Masset, Queen Charlotte Is., British Columbia to False Bay, San Juan Is., Washington, U.S.A. (type locality) (Schmitt, *et al.* 1973).

28. *Pinnixa faba* (Dana, 1851)

Distribution. Prince of Wales Is., Alaska and Puget Sound, Washington, U.S.A. (type locality) to Camalu Point, Baja California, Mexico (Zmarzly 1992).

29. *Pinnixa forficulimanus* Zmarzly, 1992

Distribution. Santa Cruz (type locality) to San Diego, California, U.S.A., depth 12 m to 46 m. (Zmarzly 1992).

30. *Pinnixa franciscana* (Rathbun, 1918)

Distribution. Middle part of the San Francisco Bay (*Albatross* sta. D5709, 37°46'37"N, 122°26' 21"W), California, U.S.A. (type locality) to Tortugas Bay, Baja California Sur. (Garth and Abbott 1980; Zmarzly 1992).

31. *Pinnixa fusca* Glassell, 1935

Distribution. San Felipe, Baja California, (Gulf of California), Mexico (type locality) (Glassell 1935b).

32. *Pinnixa hendrickxi* Salgado 2015

Distribution. Isla de la Piedra, Mazatlán, Mexico (type locality) (Salgado-Barragán 2015).

33. *Pinnixa hiatus* Rathbun, 1917

Distribution. Goleta and the Channel Is., off Santa Catalina I. (type locality) and San Diego California, U.S.A. Depth 27–100 m (Zmarzly 1992).

34. *Pinnixa huffmanii* Glassell, 1935

Distribution. Puerto Peñasco (type locality) and Las Casitas, Sonora, (northern Gulf of California), Mexico (Glassell 1935b; Hendrickx 1995).

35. *Pinnixa littoralis* Holmes, 1895

Distribution. Sitka, Alaska, U.S.A., to Santa Maria Bay (10 km south of San Quintín), Baja California, Mexico (Schmitt 1921; Campos-González 1986); intertidal to 91 m (Hart, 1982). Bodega Bay, California, U.S.A. (type locality).

36. *Pinnixa longipes* Lockington, 1876

Distribution. Bodega Bay, and Tomales Bay (type locality), California, U.S.A., to Ensenada, Baja California, Mexico; subtidal to 128 m (Carlisle 1969; Garth and Abbott 1980).

37. *Pinnixa minuscula* Zmarzly, 1992

Distribution. Goleta, Santa Barbara County to San Diego, California, U.S.A. (type locality); depth 27–50 m (Zmarzly 1992).

38. *Pinnixa occidentalis* Rathbun, 1893

Distribution. South of Unimak Island, Alaska. U.S.A., Albatross Sta. 3216, 54°20'30"N 163°27'00"W, (type locality) to Bahía Magdalena, west coast of Baja California Sur, Mexico; intertidal to 436 m (Hart, 1982); also reported from the Gulf of California, no locality specified (Glassell 1934).

39. *Pinnixa pambertoni* Glassell, 1935

Distribution. San Felipe, Baja California, (Gulf of California), Mexico (type locality) (Glassell, 1935). Record to Mazatlán Bay by Hendrickx (1995) is a confirmed misidentification of an undescribed species.

40. *Pinnixa plectrophoros* Glassell, 1935

Distribution. Puerto Peñasco, Sonora, (Gulf of California), Mexico (type locality) (Glassell 1935b).

41. *Pinnixa richardsoni* Glassell, 1936

Distribution. Laguna Superior, inlet front to Santa Maria Xadani, Juchitan de Zaragoza, Oaxaca, Mexico to Balboa, Canal Zone, Panama (type locality) (Campos *et al.* 1998).

42. *Pinnixa scamit* Martin & Zmarzly, 1994

Distribution. Western Santa Barbara Channel, SSW of Point Arguello, California, U.S.A., (type locality) and Todos Santos Bay, Baja California, Mexico (Campos *et al.* 1998).

43. *Pinnixa schmitti* Rathbun, 1918

Distribution. Port Levasheff, Unalaska, Alaska to San Diego, California, U.S.A. San Francisco Bay, California (type locality) (Schmitt *et al.* 1973; Hart 1982). Record to Mazatlán Bay by Hendrickx (1995) is a confirmed misidentification of an undescribed species.

44. *Pinnixa tomentosa* Lockington, 1877

Distribution. Monterey, California, U.S.A., to Cape San Lucas, Baja California Sur, Mexico; off San Felipe and Los Angeles Bay (type locality), Baja California and Point La Choya, Sonora (Gulf of California), Mexico (Scanland & Hopkins 1978).

45. *Pinnixa transversalis* (H. Milne Edwards & Lucas, 1844)

Distribution. Campo Don Abel, 20 km north of San Felipe and Consag Rock, Baja California and Puerto Peñasco, Sonora, (Gulf of California), Mexico, to Coquimbo, Chile; '...côtes du Chili...' (type locality); Galapagos Is.; questionably to Valparaíso, Chile, and beyond (Schmitt *et al.* 1973; Hendrickx 1995; present study).

46. *Pinnixa tubicola* Holmes, 1895

Distribution. Alaska, U.S.A.; Prince Rupert, British Columbia, Canada; Trinidad (type locality) to San Diego, California, U.S.A. and Bahía Blanca, Baja California, Mexico. (Garth & Abbott 1980; Zmarzly 1992).

47. *Pinnixa weymouthi* Rathbun, 1918

Distribution. Monterey Bay (type locality) and Pacific Grove, California (Zmarzly 1992).

***Pinnixulala* Palacios-Theil, Cuesta & Felder, 2016**

48. *Pinnixulala valerii* (Rathbun, 1931)

Distribution. Lobos Bay, Cájeme, Sonora (Gulf of California) and El Verde estuary, Sinaloa, Mexico; San Lucas Is., west coast of Costa Rica (type locality) to Colombia (Campos-González & Campoy-Favela 1987; Lemaitre & Alvarez León 1992).

***Pinnaxodes* Heller, 1865**

49. *Pinnaxodes gigas* Green, 1992

Distribution. Bajo Macho, northeast of Consag Rock, (northern Gulf of California) and Tastiota estuary, Sonora, Mexico (type locality). West coast of Baja California, near San Quintín, Baja California, Mexico (Green 1992; Campos *et al.* 1998; Emparanza *et al.* 2011; present study).

***Pinnotheres* Bosc, 1802**

50. *Pinnotheres nudus* Holmes, 1895

Distribution. Santa Cruz, California, U.S.A. (type locality) (Holmes 1895, 1900).

51. *Pinnotheres pichilinguei* Rathbun, 1923

Distribution. Pichilingue, La Paz Bay, Baja California Sur (southern Gulf of California), Mexico (type locality) (Rathbun 1923).

52. *Pinnotheres pugettensis* Holmes, 1900

Distribution. Spider Anchorage, British Columbia, Canada; Puget Sound (type locality), Washington, Monterey Bay and King Harbor, Los Angeles County, California, U.S.A. (Wicksten 2012).

53. *Pinnotheres taylori* Rathbun, 1918

Distribution. Quatsino Sound (50°30.4'N, 127°43.1'W), Ucluet, Vancouver Is., British Columbia (type locality), to Puget Sound, Washington; from 11 to 64 m. (Rathbun 1918; Hart 1982).

***Scleroplax* Rathbun, 1893**

54. *Scleroplax granulata* Rathbun, 1893

Distribution. Roller Bay, Vancouver Is., Canada to Ensenada, Baja California (type locality), San Quintín, Baja California and El Coyote Estuary, Abrejos Point, Baja California Sur, Mexico. (Campos 2006).

***Tumidothere* Campos, 1989**

55. *Tumidothere orcutti* (Rathbun, 1918)

Distribution. Manzanillo, Colima, Mexico (type locality) to Cabo Blanco Is., Costa Rica (Campos & Vargas-Castillo 2013).

56. *Tumidothere margarita* (Smith, 1869)

Distribution. Playa Kino Viejo, Sonora (Gulf of California), Mexico and from Scammon's Lagoon, Guerrero Negro, west coast of Baja California Sur, Mexico to Panama Bay, Panama (type locality) (Schmitt *et al.* 1973; Campos 1989b; present study).

***Orthotheres* Sakai, 1969**

57. *Orthotheres unguifalcula* (Glassell, 1936)

Distribution. Puerto Peñasco, Sonora, (Gulf of California), Mexico (type locality) (Campos 1989a).

***Raytheres* Campos, 2004**

58. *Raytheres clavapedatus* Glassell, 1935

Distribution. San Felipe, Baja California (type locality), (Gulf of California) to Magdalena Bay, west coast of Baja California Sur, Mexico (Campos 2004).

59. *Raytheres lithodomi* Smith, 1870

Distribution. Magdalena Bay, west coast of Baja California Sur, Mexico to Pearl Is., Bay of Panama (type locality) (Campos 2004).

***Tetrias* Rathbun, 1898**

60. *Tetrias scabripes* Rathbun, 1898

Distribution. Cerralvo Channel, San Miguel Cape, Santa Barbara, California, U.S.A.; Mita Point and southern part of Gulf of California, Albatross, Sta. 2826, 24°12'00"N, 109°55'00"W (type locality), Mexico; Coco Is., Costa Rica (Hendrickx 1995; Vargas-Castillo & Wehrtmann 2008).

Materials and methods

Specimens that represent new records were collected along the west coast of Baja California and the Gulf of California, Mexico during the past twenty years. The crabs were preserved in ethanol and deposited in the Laboratorio de Invertebrados, Facultad de Ciencias of the Universidad Autónoma de Baja California (Ensenada). Additional voucher specimens studied came from the Museum of Zoology, University of Costa Rica (MZ–UCR). Photos were taken with a digital Leica DC200 and drawings were made with the aid of a Leica Camera Lucida. Both devices were attached to a Leica MZ-12 stereoscopic microscope. Additional photos were taken with a Fujifilm-finepix S2 pro. Photos and drawings were edited using Adobe Illustrator CS and Adobe Photoshop CS. Abbreviations used: cl, carapace length and cw, carapace width.

Taxonomy

Family Pinnotheridae de Haan, 1833

Genus *Fabia* Dana, 1851

***Fabia subquadrata* Dana, 1851**

(Figs. 1A–C, E, 2B)

Material examined and new hosts. 1 female (hard stage), El Coyote Estuary, Punta Abreojos, Baja California Sur, Mexico, 26°48'43.62"N, 113°27'54.98"W, 16 July 1999, free-living; 1 adult female, intertidal, Los Bungalos, Tortugas Bay, Baja California Sur, Mexico, 27°41'55.52"N, 114°52'45.45"W, 8–9 April 2000, in *Modiolus capax*.

Revised distribution. Akutan Pass, Alaska, U.S.A. to El Coyote Estuary, Punta Abreojos, Baja California Sur, Mexico (Campos 1996).

Hosts. Common hosts include the following bivalves: *Modiolus capax*, *M. modiolus* (Linnaeus, 1758), *Mya arenaria* Linnaeus, 1758, *Mytilus californianus* Conrad, 1837, and *M. edulis* Linnaeus, 1758. Occasional hosts include: *Cyclocardia ventricosa* (Gould, 1850), *Leukoma staminea* (Conrad, 1837), *Saxidomus gigantea* (Deshayes, 1839), *Tivela stultorum*, *Tresus capax* (Gould, 1850), and *T. nuttallii* (Conrad, 1837) (Pearce 1966; Garth & Abbott 1980; Campos 1996).

Other hosts. Garth & Abbott (1980) recorded the Atlantic bivalve *Cyclocardia borealis* (Conrad, 1832) as an occasional host; however, the presence of this bivalve in the eastern Pacific should be confirmed. The record of *Mytilus edulis* also needs confirmation because this species is validly reported only from embayments in California U.S.A. Mytilids from open coastal area may belong to *M. galloprovincialis* Lamarck, 1819, or *M. trossulus* Gould, 1850 (D. B. Cadien, pers. comm.).

Remarks. Species of *Fabia* can be separated from other genera of Pinnotheridae by the possession in adult females of two deep sulci on the carapace that extend from the orbit to the gastric region (Fig. 1A) and males having a smooth, shiny, porcelain-like carapace and two or more fused abdominal somites (Campos 1996). Four species have so far been recorded from the eastern Pacific: *Fabia carvachoi* Campos, 1996, *F. concharum* (Rathbun, 1893), *F. malaguena* (Garth, 1948), and *F. subquadrata*. Both *F. subquadrata* and *F. concharum* overlap in their distribution and may inhabit the same host in Southern California, U.S.A. and on the west coast of Baja California, Mexico. Females of both species can be separated using the morphology of the chela and third maxilliped. *Fabia concharum* has one row of setae on the ventral margin of the cheliped propodus (Fig. 2A) and the length of the dactyl of the third maxilliped is less than one-half the length of propodus (Fig. 1D). *Fabia subquadrata*, instead, has two rows of setae, one marginal and other submarginal, on the ventral region of the hand of cheliped (Fig. 2B), and the length of the dactyl of the third maxilliped is more than one-half the length of propodus (Fig. 1B, C). Males can also be separated by differences in the abdomen. Somites 2–4 are fused in *F. subquadrata*, the lateral margin of somite 5–6 with pubescence, and the telson is subcircular (Fig. 1F). In contrast, *F. concharum* has fused abdominal somites 3–5 (Rathbun, 1918; but this needs confirmation), the lateral margin of the sixth somite is hairless, and the telson is subtrapezoidal (Fig. 1E). Campos (1996) and Campos & Manning (1998) pointed out how these species can be separated from the Pacific Ocean congeners *F. carvachoi* of the Gulf of California, Mexico and *F. malaguena* of Malaga Bay, Colombia.

The present record extends the southern distribution limit of *F. subquadrata* approximately 600 km from Ejido Eréndira, Baja California to El Coyote Estuary, Abreojos Point, Baja California Sur, Mexico and adds *Modiolus capax* as a new host for the adult female. Other pinnotherids commonly found in the mantle cavity of *M. capax* include *Opisthopus transversus* and *F. concharum*. This last species only has been recorded subtidally in Todos Santos Bay, Baja California and Tortugas Bay, Baja California Sur, both localities located on the west coast of Baja California (Campos *et al.* 1992; pers. obs.). *Fabia subquadrata* commonly is found in the mantle cavity of the mussel *Mytilus californianus* in California, U.S.A. and Baja California; nevertheless, *M. modiolus* is the common host in Puget Sound, Washington, U.S.A (Pearce 1966).

Genus *Opisthopus* Rathbun, 1893

***Opisthopus transversus* Rathbun, 1893**

(Figs. 3F–I, 4A–D)

Material examined and new hosts. 1 female, Nov. 2014, from commercial catches, Ensenada shellfish market, collected in Punta Colonet, Ensenada, Baja California, Mexico (30°57'43.65"N, 116°19'22.44"W) in *Tivela stultorum*.

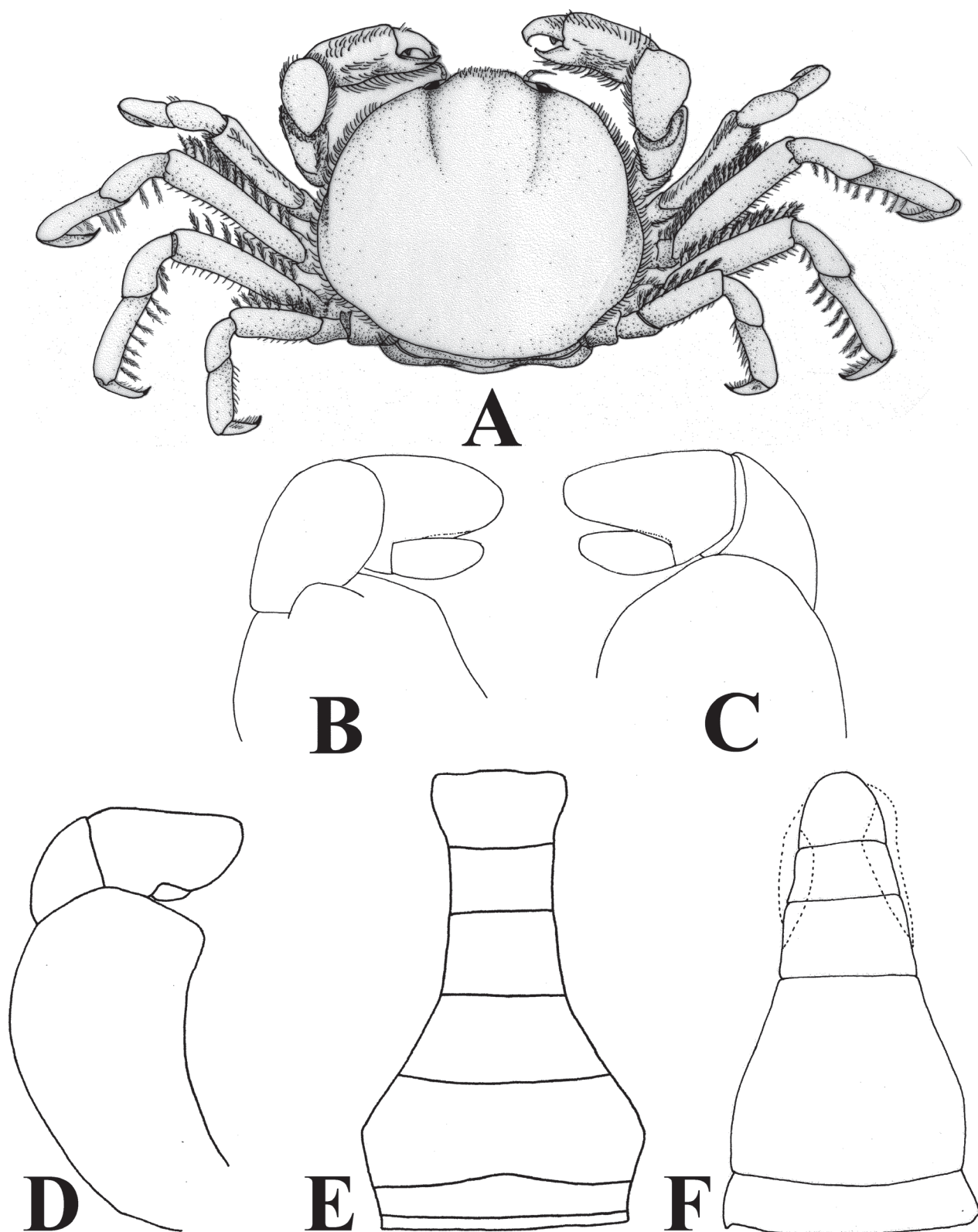


FIGURE 1. A–C, E, *Fabia subquadrata* Dana, 1851 from Todos Santos Bay, Ensenada, Baja California, Mexico: A, Female dorsal view, carapace width 6.7 mm; B–C, third maxilliped of female, carapace width 18.3 mm, inner and outer view respectively; F, male abdomen, carapace width 9.5 mm, dots indicate the area covered by setae. D–E, *F. concharum* (Rathbun, 1853) from California, U.S.A.: D, third maxilliped outer view, x 30; E, male abdomen, x 15. C–D after Davidson (1968).

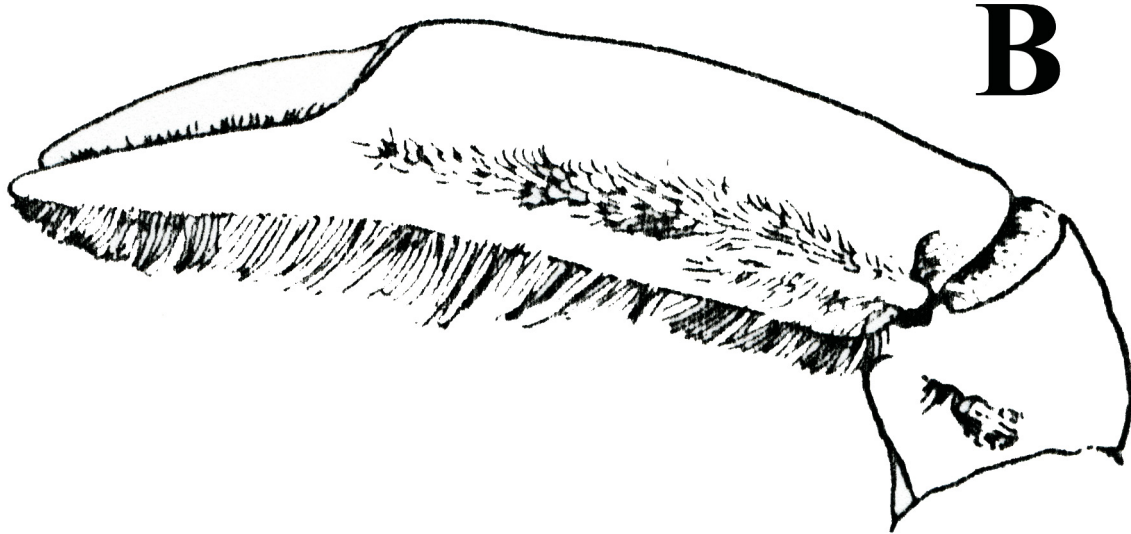
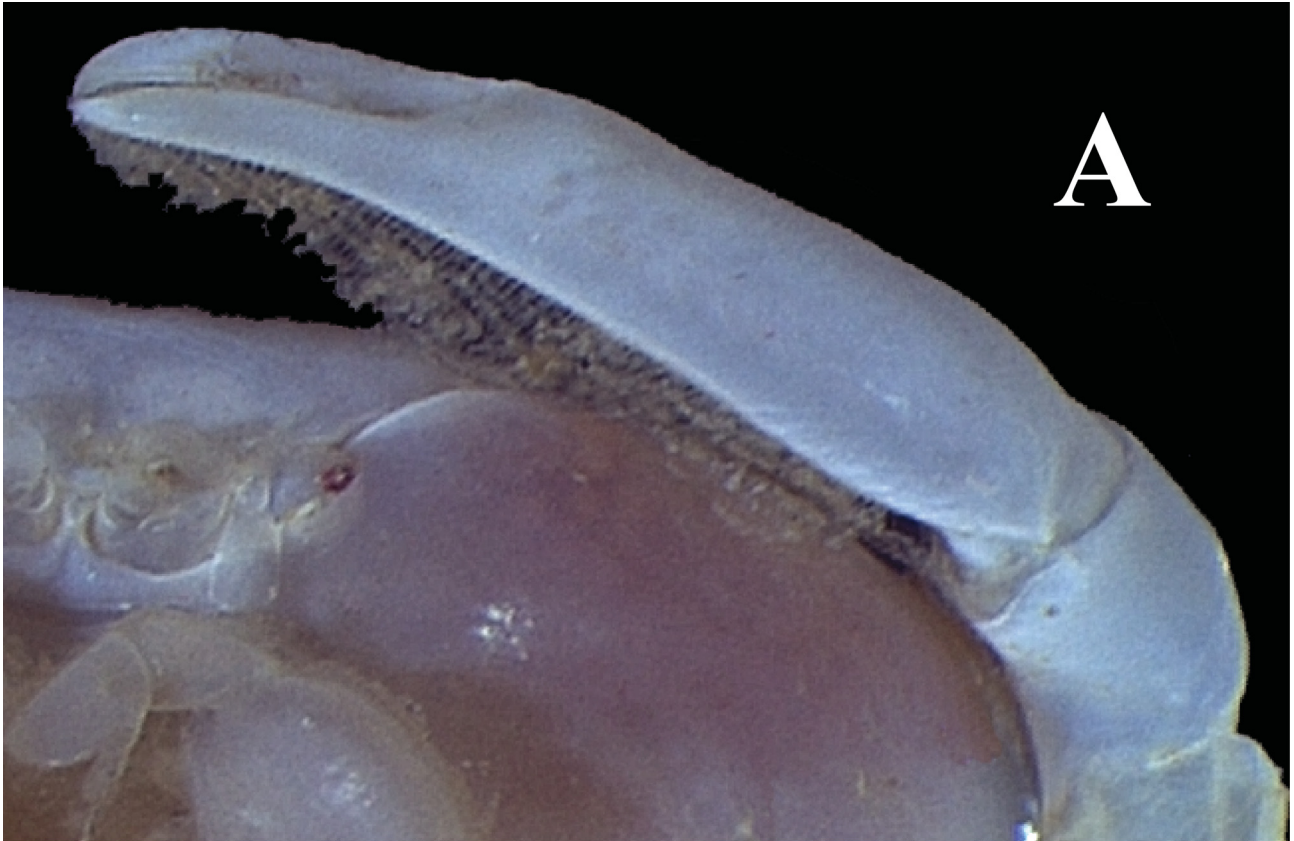


FIGURE 2. A, *Fabia cocharum* (Rathbun, 1853), female showing one line of setae on the ventral margin of the propodus, carapace width 13.4, San Vicente, Ensenada, Baja California, Mexico; B, *F. subquadrata* Dana, 1851, female showing two lines of setae, one submarginal and second on ventral margin of the propodus, carapace width 6.7 mm, Todos Santos Bay, Ensenada, Baja California, Mexico.

Distribution. Santa Cruz, California, U.S.A to Laguna de San Ignacio, Baja California Sur, Mexico (Campos & Manning 2000).

Hosts. Symbiont in the giant Pacific chiton *Cryptochiton stelleri* (von Middendorff, 1847); the gastropods *Aplysia vaccaria* Winkler, 1955, *Bulla gouldiana* Pilsbry, 1895, *Conus californicus* Reeve, 1844, *Lithopoma undosum* (Wood, 1828) [= *Megastraea undosa* (W. Wood)], *Megathura crenulata* (Sowerby I, 1825), *Navanax inermis* (J. G. Cooper, 1862), and *Neverita lewisii* (Gould, 1847); the bivalves *Atrina tuberculosa* (G. B. Sowerby I, 1835), *Crassadoma gigantea* (J.E. Gray, 1825), *Crassostrea gigas* (Thunberg, 1793), *Megapitaria squalida* (G. B.

Sowerby I, 1835), *Modiolus capax*, *Modiolus* sp., *Mytilus edulis* (see below), *Nuttallia nuttallii*, *Pholas* sp., *Platyodon* sp., *Pseudochama exogyra* (Conrad, 1837), *Tivela stultorum*, *Tresus nuttallii*, *Zirfaea* sp., and *Zirfaea pilsbryi* Lowe, 1931. Also commensal in the tube of the polychaete *Chaetopterus variopedatus* (Renier, 1804), and the cloaca of the holothuroids *Apostichopus californicus* (Stimpson, 1857), *A. parvimensis* (Clark, 1913), and *Molpadia arenicola* (Stimpson, 1857), (Schmitt *et al.* 1975; Garth & Abbott 1980; Ricketts *et al.* 1980; Campos *et al.* 1992).

Other hosts. Garth & Abbott (1980) recorded the species in the Atlantic bivalve *Dinocardium robustum* (Lightfoot, 1786), but the presence of this bivalve in the eastern Pacific should be confirmed. Likewise, the record of *Mytilus edulis* needs confirmation since this species is validly reported only from embayments in California U.S.A. Mytilids from open coastal area may belong to *M. galloprovincialis* or *M. trossulus*.

Remarks. According to Hopkins & Scanland (1964) the occurrence of *O. transversus* in multiple host species is evidence of the non-specificity of this pinnotherid. Although this conclusion is evident, another interpretation is that the species needs more than one host to complete its life history. The generalist behavior along the life history of *O. transversus* probably involves a complex relationship with their invertebrate hosts. Host selection is most probably not by chance. Thus, following Hopkins & Scanland (1964) it is possible to hypothesize that young individuals of *Opisthopus* infest a temporary host like the giant Pacific chiton *Cryptochiton*, moving initially to one or several larger hosts, e.g. *Lithopoma*, *Megathura*, or *Stichopus*, followed by a final selection of a definitive host, e.g. *Crassadoma*, *Molpadia*, or *Zirfaea* in which crab grow until they reach the adult phase, including ovigerous females. I concur with Hopkins & Scanland (1964) that host selection may be linked to host size, which provides space for growth and shelter; however, different hosts may also provide different types of nutrients necessary for development and reproduction.

Because *O. transversus* was recorded in the Gulf of California (Glassell 1935a), for the past 20 years I have examined potential hosts in beaches around San Felipe, Puertecitos, and Bahía de Los Angeles, Gulf of California, Mexico, including species of Mytilidae, Veneridae, Solecurtidae, Cardidae, and Hiatellidae, but no pinnotherid assignable to this species have been collected. The juvenile males recorded by Glassell, which were unavailable for study, may belong to *Pinnaxodes gigas* Green, 1992, a species that morphologically resemble *O. transversus* and inhabits the Gulf of California (see below).

Genus *Pinnaxodes* Heller, 1895

Pinnaxodes gigas Green, 1992

(Figs. 3A–E)

Material examined. 1 male, Bajo Macho, northeast of Consag Rock, upper Gulf of California, Mexico, 31°7'26.38"N, 114°31'50.68"W, May 1995, shrimp trawl; 1 female, Kino Bay, Sonora Mexico, 28°48'33.66"N, 111°54'59.26" W in *Pinna rugosa*; 10 females, west coast of Baja California, near San Quintín, 30°28'31.58"N, 116°4'30.27"W, 19 Dec. 2011, in *Panopea* sp. (presumably *P. generosa*, see below).

Distribution. Gulf of California: Bajo Macho, northeast of Consag Rock, upper Gulf of California; Tastiota estuary, Sonora, Mexico. West coast of Baja California, commercial catches near San Quintín, Baja California, Mexico (Green 1992; Campos *et al.* 1998; Emparanza *et al.* 2011; this work).

Hosts. Gulf of California: the bivalves *Panopea globosa* (Dall, 1898), *Pinna rugosa* (Sowerby, 1835) (new host) and west coast of Baja California *Panopea* sp., presumably *P. generosa* (new host), (Emparanza *et al.* 2011; this work).

Remarks. The geoduck crab *Pinnaxodes gigas* is the largest pinnotherid crab ever recorded for the Americas, with fully developed female having a carapace width of up to 36 mm. Examination of recently dead specimens permitted corroborating the color pattern reported by Green (1992) and Campos *et al.* (1998): red orange spots (hexadecimal color # d13c00) on the dorsal surface of carapace and ambulatory legs, whereas the ventral surface has shades of dark grayish orange (hexadecimal color #a89d94) (Fig. 3A). Other species including *P. floridensis*, from the Northwestern Atlantic, and *Opisthopus transversus*, from the Eastern Pacific, feature such red-spots as well, which Hopkins & Scanland (1964) explained as crabs eating carotenoid-food rich from their host. These species share a suborbicular to subpentagonal carapace, a third maxilliped with a spoon-shaped dactylus

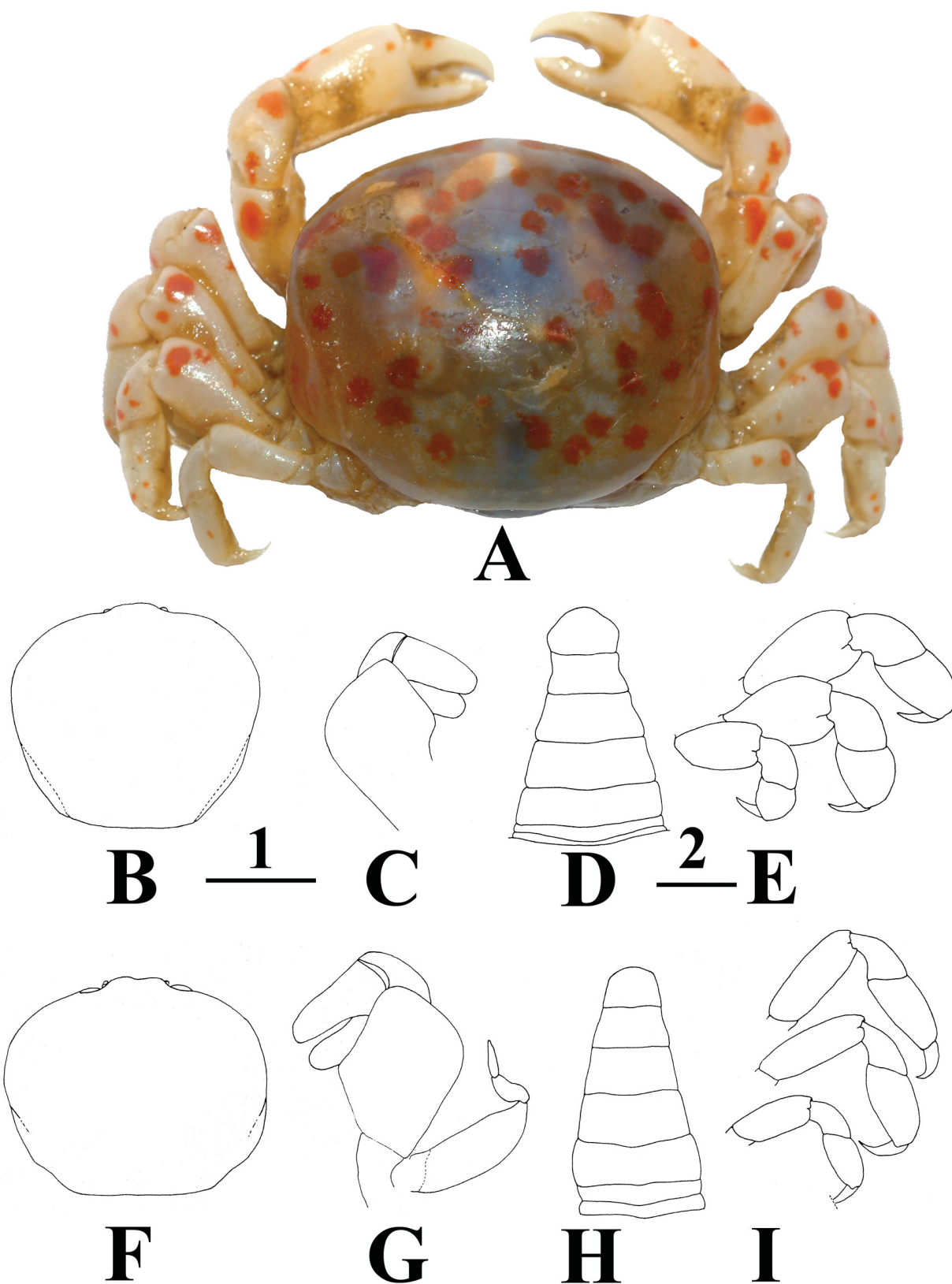


FIGURE 3. A–E, *Pinnaxodes gigas* Green, 1992, A, near San Quintín, Baja California, Mexico; B–E, San Felipe, Baja California, Mexico: adult female A, dorsal view, carapace width 28.4 mm; adult male, B, carapace, dorsal view; C, third maxilliped, outer view; D, abdomen; E, pereopods 3–5 (ambulatory legs 2–4). *Opisthopus transversus* Rathbun, 1893 adult male, Ensenada, Baja California, Mexico: F, carapace, dorsal view; G, third maxilliped, outer view; H, abdomen; I, pereopods 3–5 (ambulatory legs 2–4). Scale 1: B, 3.4 mm; C, 0.4 mm; F, 1.27 mm; G, 0.36 mm. Scale 2: D, 1.46; E, 2.17; H, 0.73; I, 1.27.

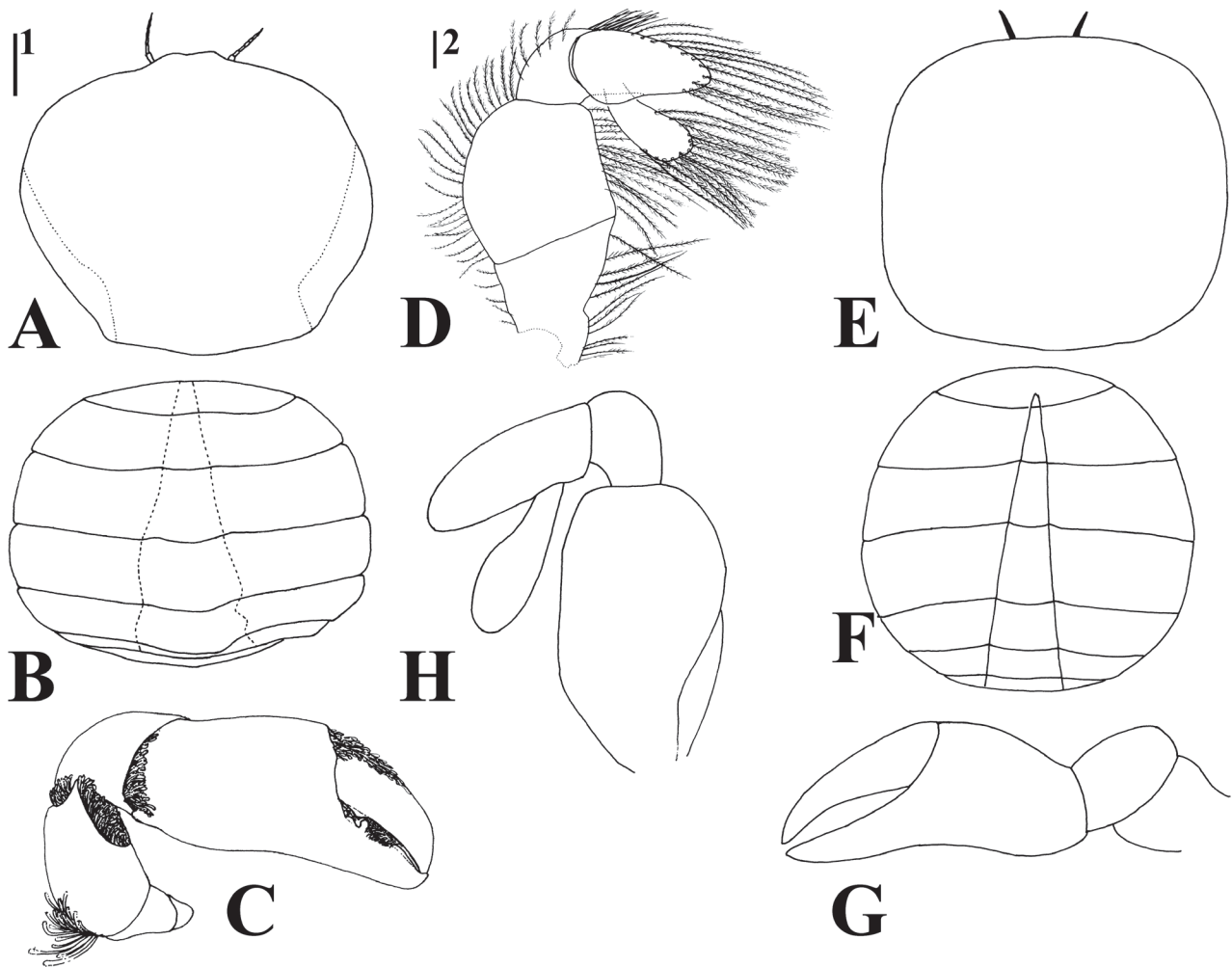


FIGURE 4. A–D, *Opisthopus transversus* Rathbun, 1918 from Punta San Miguel, Todos Santos Bay, Ensenada, Baja California, Mexico. E–H, *Pinnotheres nudus* Holmes, 1895, from Santa Cruz, California, U.S.A. Adult female: A, E, carapace, dorsal view; B, F, abdomen; C, G, right and left cheliped respectively, outer aspect; D, H, third maxilliped, outer view. A–C, scale 1: 0.5 mm; 2: 0.1 mm; E–H, not to scale.

proximally inserted on the spatulate propodus, and males with a narrow and triangular abdomen (Figs. 3B–D, F–H). There are nevertheless morphological differences between these species of *Pinnaxodes* and *O. transversus*, including the shape of the front, and the meri of ambulatory legs and telson (Campos *et al.* 1998). *Pinnaxodes gigas* and *P. floridensis* have entire the front, meri of ambulatory legs distally swollen, and telson of the males basally expanded (Fig. 3B–E). *Opisthopus transversus*, in contrast, has an emarginate front, meri of ambulatory legs uniformly wide, and telson of the males not basally expanded (Fig. 3F–I). Despite females of *P. gigas* being undescribed, the male diagnostic features of the front and ambulatory legs can be used to separate females of *P. gigas* from females of *O. transversus* (pers. obs.).

The present record of *P. gigas* in *Pinna rugosa* is unusual. Several decapod symbionts are known from *P. rugosa*, including the pontonine shrimps *Pontonia pinnae* Lockington, 1878, and *P. simplex* Holthuis, 1951 (Wicksten 1983, 1989; Campos *et al.* 1995; Paredes-Rios & Balart 1999). The published host data suggests that the preferred host for *P. gigas* in the Gulf of California is *Panopea globosa*, (Emparanza *et al.* 2011; pers. obs.). The strong and firm carapace, chelipeds, and ambulatory legs of this crab are shared with pinnotherids that evolved to live in symbiosis with sea cucumbers, e.g. *Pinnixa banharti* Rathbun, 1918 (host *Molpadia arenicola*) or *Holothuriophilus trapeziformis* (Burger, 1895) (host *Holothuria inornata* Semper, 1868) (Hopkins & Scanland 1964; Campos 2007; Campos *et al.* 2012). Campos *et al.* (1998) suggested a sea cucumber as a potential host for *P. gigas*. The robust morphology of this crab allows to hypothesize that a host change probably occurred in *P. gigas*, first evolving as a symbiont in the cloaca of a sea cucumber, switching later to a geoduck clam, a burying bivalve

that is characterized by large and fused siphons that resemble the body-shape of a sea-cucumber. The strong and firm body of *P. gigas* does not match the soft carapace and weak pereopods of pinnotherids that evolved as symbionts of bivalves, e.g. species in Pinnotherinae *sensu stricto* (Campos 2009). It therefore possible that geoducks clams, *Panopea* spp., have been more recently exploited as hosts of *P. gigas*.

According to Emparanza *et al.* (2011) *P. globosa* from Playa del Sol (open coast), Empalme, Sonora, Mexico were infested with at least one crab each, infestation rate being 100%, but some clams were infested by heterosexual pairs or even three individuals per host recording an average of 1.4 crabs by host. Conversely, a population of *P. globosa* from Altata lagoon system, Sinaloa, Mexico was uninfested by *P. gigas* (Góngora-Gómez *et al.* 2016; pers. comm). Cáceres-Martínez & Vásquez-Yeomans (2008) recorded an unidentified pinnotherid crab in *P. generosa*, presumably *P. gigas*. Because the known distribution of geoducks in Baja California is putatively disjunct, specimens of *P. gigas* from San Quintín herein recorded were probably from *P. generosa* (see Calderon-Aguilera *et al.* 2010). The shells of the clam hosts were unfortunately destroyed and their identities were not confirmed. Confirmation of this host is desirable, since several species of subtropical and tropical species of crabs have been recently discovered in San Quintín Bay (Campos & Campos 2012). It is possible that the sub-tropical *Panopea globosa* may occur within the southern limit of *P. generosa*, between San Quintín and Canoas Point (29°25'N, 115°06'W; González-Peláez *et al.* 2013) on the west coast of Baja California. Most of the publications dealing with the distribution of *Panopea* along the west coast of Baja California cut the northern distribution of *P. globosa* at Magdalena Bay, with only one extralimital record by González-Peláez *et al.* (2013), and the southern distribution of *P. generosa* in San Quintín-El Tomatal (28°29'9.75"N, 114°4'1.60"W) (Aragón-Noriega *et al.* 2012; González-Peláez *et al.* 2013; pers. obser.). Both species may nevertheless overlap their distribution between Magdalena Bay and El Tomatal on the west coast of the Baja California, a transitional biogeographic region for marine biota of the Californian, Mexican, and Cortez provinces (Brusca & Wallerstein 1979) that is periodically affected by El Niño and La Niña oscillations (Wang & Fielder 2006). This may influence the distribution of species of the region including species of *Panopea* and their symbionts (see Campos & Campos 2012).

Genus *Pinnotheres* Bosc, 1802

Pinnotheres nudus Holmes, 1895

(Figs. 4 E–H)

Diagnosis. Carapace slightly broader than long, subquadrate to orbicular in outline, convex, curving downwards towards margins, surface smooth, naked, regions not defined. Front deflexed, rounded, not protruding, central portion continued downward as triangular process between antennules, smaller triangular processes at sides partly separating orbits from antennular fossettes. Orbits ovate, wide inner hiatus partly filled by base of antennae; eye peduncles very short, stout, cornea minute. Antennules oblique; antennular fossettes communicate each other beneath front. Third maxillipeds oblique, nearly fitting buccal area; merus broad, smooth, subquadrate, outer margin produced into broadly rounded laminate expansion; propodus oblong, distally rounded; dactylus spatulate, articulated near base, extending somewhat beyond propodus. Chelipeds moderate, smooth, naked; hands narrow, rather thick, widest immediately behind articulation of dactyl; fingers nearly or quite as long as palm, subconical, not conspicuously dentate on inner margins, partly covered by very short, dense pubescence. Pereiopods 2–4 subequal, pereopod 5 smaller, all smooth, little compressed, dactyli acute, nearly straight, those pereopod 5 longer, more slender than preceding pairs. Abdomen of female nearly circular in outline, covers entire sternal surface; six somites and telson separated, fourth, fifth and sixth being subequal, larger than others (modified from Holmes, 1895).

Distribution. Santa Cruz (type locality), Monterey, California, U.S.A. (Holmes 1895, 1900).

Hosts. Unknown.

Remarks. *Pinnotheres nudus* is known by its original description based on two syntype females collected at Santa Cruz, California, U.S.A. The two syntypes deposited in the California Academy of Sciences were destroyed in the San Francisco fire after the earthquake of April 18, 1906. Measurements of the syntypes given by Holmes (1895) (cl 20 mm, cw 24 mm; cl 15.5 mm, cw 19 mm). For more than a century there have been no new published records for this species. Campos & Manning (2000) nevertheless suggested that *P. nudus* should be placed in

synonymy with *Opisthopus transversus*. Both species share several features including a large antenna, visible dorsally (Fig 4A, E), a third maxilliped with a carpus that is shorter than the spatulate propodus, and a spoon-shaped dactylus that is inserted proximally on the ventral margin of the propodus, with its apex extending beyond the tip of this article (Fig. 4D, H). Both species possess pereopods 2–4 that are subequal in length and shape, whereas the pereopods 5 are the shortest. Furthermore, the abdomen (Fig 4B, E) is nearly circular, composed of six somites and a freely articulating telson, with somites 4–6 subequal and larger than the others. Although these shared features may suggest that both species are synonymous, a reappraisal of their morphology showed some important features that were overlooked by Campos & Manning (2000). *Pinnotheres nudus* has a front that is deflexed, rounded, not protruding (Fig. 4E), the central portion continued downward as a triangular process between the antennules; the subconical fingers of the chela are not conspicuously dentate along the inner margins, and although described as long as the palm, the original figure shows that both pollex and dactylus are longer than the palm (Fig. 4G), and the dactyli of pereopods 2–4 are acute, nearly straight whereas those of pereopods 5 are relatively longer and more slender than in the preceding pairs. In contrast, *O. transversus* has a slightly produced, deflexed, almost straight, emarginate front (Fig. 4A); the fingers of the chela are shorter than the palm and the cutting edge of the fingers has one small tooth at the base of dactylus and two or three at base of the pollex (Fig. 4C), and the dactyli of pereopods 2–4 are uniformly curved and small, whereas the dactyli of the pereopods 5 are no longer than those of pereopods 2–4 and all are of similar shape. These features allow to clearly distinguish both species so *P. nudus* should be removed from the synonymy of *O. transversus* and considered a valid species. The morphology of the third maxilliped described above and the shape and relative length of the dactyli of pereopods 2–5 support the exclusion of *P. nudus* from *Pinnotheres* Bosc, 1802. The species is nevertheless retained temporarily in *Pinnotheres* awaiting the collection of additional material.

Genus *Tumidotheres* Campos, 1989b

Tumidotheres margarita (Smith, 1870)

(Figs. 5 C, D)

Material examined. Gulf of California: 2 females (1 juvenile, 1 gravid), Playa Kino Viejo, Sonora, 28°75'N, 112°00'W, 24 Jan 1985, in *Argopecten irradians concentricus* (Say, 1822); 2 females (1 ovigerous), 24 Jan 1985, in *A. i. concentricus*; 1 ovigerous, 2 May 1983, in *Pinctada mazatlanica* (Hanley, 1855); 1 female, 18 May 1984, in *P. mazatlanica*; 3 females (2 ovigerous), 4 Nov. 1984, in *P. mazatlanica*, Punta San Pedro, Bahía Concepción, Baja California Sur, 26°49'46.95"N, 111°52'19.21"W. West coast of Baja California: 4 males and 30 females, 4 April 1987, Estero El Cardón, Laguna de San Ignacio, Baja California Sur, 26°47'40.38"N, 113°9'4.49"W, in *Argopecten ventricosus* (G. B. Sowerby II, 1842); 4 males (2 juveniles), 2 females (1 ovigerous) Banco El Zacatoso, Laguna Ojo de Liebre, Guerrero Negro, Baja California Sur, Mexico, 27°53'05"N; 114°08'39"W, 9 Jan 2013 in *Nodipecten subnodosus* (G. B. Sowerby I, 1835) (new host); 2 females juveniles, Banco La Concha, Laguna Ojo de Liebre, Guerrero Negro, Baja California Sur, Mexico, 27°49'21"N; 114°14'25" W, 9 Jan 2013 in *N. subnodosus*.

Additional material examined. 1 ovigerous female (Museum of Zoology, University of Costa Rica, MZ–UCR 2220–11), northeast side Cabo Blanco Is., dredged parallel to the line coast, 30–40 m depth, 16–17 May 1998, Costa Rica, 9°33'26.67"N, 85°07'05.61"W.

Revised distribution. Playa Kino Viejo, Sonora, (Gulf of California) and west coast of Baja California Sur to Scammon's Lagoon, Guerrero Negro, Baja California Sur, Mexico to Panama Bay, Panama (Schmitt *et al.* 1973; Campos 1989; present record).

Hosts. Mollusca: Bivalvia: Pectinidae; *A. i. concentricus*, *A. ventricosus*, *N. subnodosus* (new host); and Pteridae, *P. mazatlanica* (Campos-González 1988; Campos 1989; present study).

Distribution and host removed. Records of *T. margarita* from El Rosario, west coast of Baja California in *Crassadoma giganteus* (Gray, 1825) and the San Felipe area, northern Gulf of California, in *Limaria pacifica* (d'Orbigny, 1846) and *Barbatia reeveana* (d'Orbigny, 1846) by Campos (1989b) are confirmed misidentifications. Their taxonomic status is to be discussed in a forthcoming publication.

Remarks. The American genus *Tumidotheres* consist of three species: the Atlantic *T. maculatus* (Say) and the Pacific *T. margarita* and *T. orcutti* (Rathbun, 1918). All these species share a swollen carapace covered with short,

dense, and deciduous tomentum, a third maxilliped with a narrowly spatulate dactylus, inserted in angular notch in middle of ventral margin of propodus; the dactyl of the last ambulatory leg being much longer than that of the other ambulatory legs in adult females, and the abdomen with six somites and a freely articulating telson. *Tumidotherees margarita*, which seems to prefer scallops (family Pectinidae), can be separated from its only known Pacific Ocean congener, *T. orcutti* (host unknown), by the unique dentition of the cutting edge of the cheliped pollex, which is armed with small teeth, all similar in size (Fig. 5C–D). In contrast, the pollex of *T. orcutti* has a blunt proximal lobe and a row of small teeth, the two distal teeth being conspicuously the largest (Fig. 5 A–B).

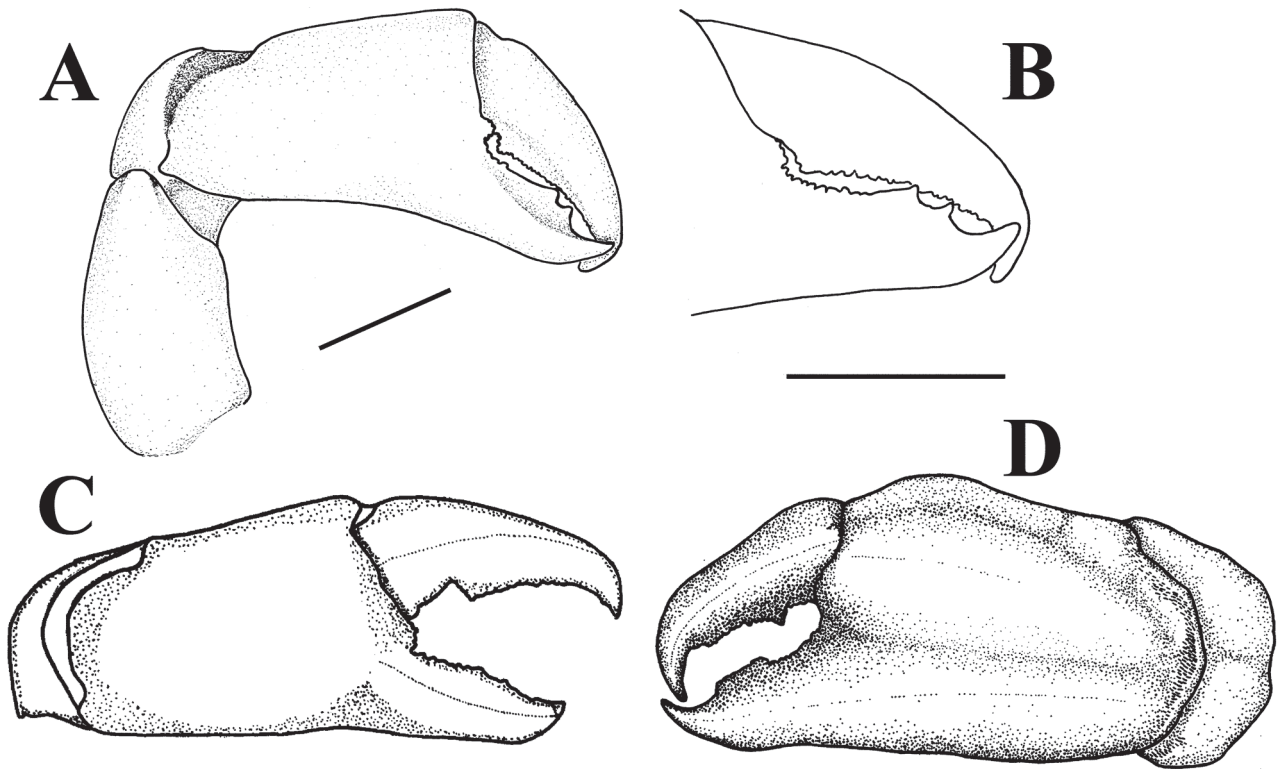


FIGURE 5. A–B, *Tumidotherees orcutti* (Rathbun, 1918) from Cabo Blanco Is., Costa Rica, female (MUCR 2220–11). A, cheliped, outer view; B, tip of cheliped; scale: 1 mm. C–D *Tumidotherees margarita* (Smith, 1870) from Magdalena Bay, Baja California Sur, Mexico: C–D, cheliped, outer view, female and male respectively. Not to scale.

Some aspects of the life history of *T. margarita* were revised by Campos (1989b), who pointed out this species develops into a hard stage crab (Christensen & McDermott 1958) after several molts of the infestive and prehard stages. Presumably, hard stage males and females leave their host to form a copulatory swarming in open sea, reinfesting their host after mating. Data from Felix-Pico (1992) suggest that *T. margarita*, found in *A. circularis*, start copulation during late winter and spring. After copulatory swarming, females re-infest their host, reaching the ovigerous stage during late spring and summer, and disappearing during autumn-winter. The discovery of males of *T. margarita*, in prehard and hard stage, and females in posthard stages (Felix-Pico 1992) suggest this crab completes its postplanktonic life history in a single host species, which is re-infested after copulation in open water. Similarly *T. maculatus* re-infests to *Mytilus edulis* after copulation in open water (Pearce 1969). The absence of females in prehard and hard stage of *T. margarita* is remarkable, which may suggest that these female stages may live in a different host that was overlooked or that the males in prehard and hard stage recorded by Felix-Pico (1992) included undetected females. Males and females in pre-hard and hard stages are identical and have a narrow abdomen, which results in them frequently being identified as males. The sexes in Pinnotheridae at prehard and hard stage can be only recognized by locating the gonopods in males (see Campos 1989b, 2013) and pleopods in females along with the presence of female gonopores on the sixth thoracic sternite and male gonopods on the eighth thoracic sternite.

Discussion

Sixty species of pinnotherid have been currently recorded for the northeastern Pacific coast of North America (Alaska to the Mexican tropical Pacific) with pinnixids (e.g. *Austinixa* Heard & Manning, 1997, *Glassella* Campos & Wicksten, 1997, *Pinnixa* White, 1846, and *Scleroplax* Rathbun, 1893) the most diverse group with 27 species (45%) and distributed in all the zoogeographic provinces included in the region. A total of 26 species (43.3 %) exclusively inhabit the Aleutian to the Californian province (*sensu* Brusca & Wallerstein 1979), 12 species (20%) are restricted to the Gulf of California (Cortez Province), and 23 species (38.3 %) are known from the tropical Pacific (Mexican and Panamic provinces), 13 of which extend their distribution into the Gulf of California and some, e.g., *Dissodactylus nitidus* and *D. xanthusi*, reaching the northern gulf during summer months (pers. obs.). The range extension and new hosts recorded herein, along with new records and new species of pinnotherid crabs described in the past few years for the tropical Pacific (Campos 2013; Campos & Vargas-Castillo 2013; Ayón & Hendrickx 2014; Salgado-Barragán 2015) strongly indicate that much more fieldwork and taxonomic study is needed to obtain a better idea of the species diversity of these inconspicuous crabs in this region. Assuming that diversity increases from north to south (see, Hendrickx *et al.* 2007), it is expected that the actual number of pinnotherids in the subtropical-tropical Mexican Pacific could be higher than that of the Aleutian, Oregonian, and Californian provinces and not so similar as is now known. Species diversity would be higher if the species endemic to the Gulf of California are added to those in the subtropical and tropical Mexican Pacific. If the actual ranges of poorly studied species were better known, one could recognize endemic species in each biogeographic province and discover extralimital distributions for species that are able to temporarily extend or contract their distribution, presumably influenced by El Niño and La Niña phenomena (Wang & Fielder 2006; Campos & Campos 2012).

Pinna rugosa is an unusual host for a pinnotherid in that it also is the common host for the caridean shrimps *Pontonia pinnae* and *P. simplex* (Wicksten 1983, 1989; Campos *et al.* 1995, Paredes-Rios & Balart 1999). It is considered to be an incidental host for *Pinnaxodes gigas*. It remains unknown if *P. gigas* will inhabit a *Pinna* individual that is already inhabited by the shrimps, or if the crab or the shrimps can displace each other or share the same particular host. Pinnotherids that inhabit several host species are generalists, but whether all these host species are required to complete their life cycle or if this can be completed in each host is unknown. In some species of pinnotherids, their interactions with one or several hosts suggest that a complex relationship may occur between the post-planktonic phases of development of the crab and different hosts (see above; Campos 2013). The record of a sole host e.g. *Holothuriophilus trapeziformis* in *Holothuria inornata* (see above; Campos *et al.* 2012) could suggest the crab is a specialist, but it would be premature to address a categorical conclusion about specialization without knowing whether the juvenile and pre-adults phases inhabit the same host. This is also applicable to other pinnotherid or symbiotic crustaceans in general, which are known only from the adult phase of development from a single host species, and the potential hosts of juvenile and subadult phases remain unknown.

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References

- Anker, A., Murina, G.V., Lira, C. Caripe, J.A.V., Palmer, R. & Jeng, M.S. (2005) Macrofauna associated with echiuran burrows: a review with new observations of the innkeeper worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela. *Zoological Studies*, 44, 157–190.
- Anonymous (2012) Callo de hacha. In: Anonymous. (Ed.), *Carta Nacional Pesquera (Segunda Sección)*. Diario Oficial de la Federación, Mexico, pp. 26. Available from: <http://www.inapesca.gob.mx/portal/documentos/publicaciones/carta-nacional-pesquera/Carta-Nacional-Pesquera-2012.pdf> (accessed 13 August 2016)
- Aragón-Noriega, E.A., Alcántara-Razo, E., Calderón-Aguilera, L.E. & Sánchez-Fourcade, R. (2012) Status of geoduck clam fisheries in Mexico. *Journal of Shellfish Research*, 31, 733–738.
<http://dx.doi.org/10.2983/035.031.0317>
- Ayón-Parente, M. & Hendrickx, M.E. (2014) *Calyptraeotheres* sp. nov. (Crustacea: Decapoda: Pinnotheridae), symbiont of the slipper shell *Crepidula striolata* Menke, 1851 (Mollusca: Gastropoda: Calyptraeidae) from the Gulf of California, Mexico. *Zootaxa*, 3872 (1), 89–94.
<http://dx.doi.org/10.11646/zootaxa.3872.1.8>
- Brusca, R.C. & Wallerstein, B.R. (1979) Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow–water zoogeography for the region. *Bulletin of the Biological Society of Washington*, 3, 67–105.
- Cáceres-Martínez, J. & Vásquez-Yeomans, R. (2008) La patología en moluscos bivalvos: principales problemas y desafíos para la producción de bivalvos en América Latina. In: Lovatelli, A., Farias, A. & Uriarte, I. (Eds.), *Estado actual del cultivo y manejo de moluscos bivalvos y su proyección futura: factores que afectan su sustentabilidad en América Latina. Taller Técnico Regional de la FAO, 20–24 de agosto de 2007, Puerto Montt, Chile*. FAO, Actas de Pesca y Acuicultura, Roma, pp. 327–337
- Calderón Aguilera, L.E., Noriega, E.A.A., Hand, C.M. & Rivera, V.M.M. (2010) Morphometric relationships, age, growth, and mortality of the geoduck clam, *Panopea generoa*, along the Pacific coast of Baja California, Mexico. *Journal of Shellfish Research*, 29, 319–326.
<http://dx.doi.org/10.2983/035.029.0206>
- Campos, E. (1989a) Comments on taxonomy of the genus *Orthootheres* Sakai, 1969 (Crustacea, Brachyura, Pinnotheridae). *Bulletin of Marine Science*, 44, 1123–1128.
- Campos, E. (1989b) *Tumidootheres*, a new genus for *Pinnotheres margarita* Smith, 1869, and *Pinnotheres maculatus* Say, 1818 (Brachyura: Pinnotheridae). *Journal of Crustacean Biology*, 9, 672–679.
<http://dx.doi.org/10.1163/193724089X00674>
- Campos, E. (1993) Systematics and taxonomic remarks on *Pinnotheres muliniarum* Rathbun, 1918 (Crustacea: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 106, 92–101.
- Campos, E. (1996) Partial revision of pinnotherid crab genera with a two-segmented palp on the third maxilliped (Decapoda: Brachyura). *Journal of Crustacean Biology*, 16, 556–563.
<http://dx.doi.org/10.1163/193724096X00595>
- Campos, E. (2002) Two new genera of pinnotherid crabs from the tropical eastern Pacific (Decapoda: Brachyura: Pinnotheridae). *Journal of Crustacean Biology*, 22, 328–336.
<http://dx.doi.org/10.1163/20021975-99990239>
- Campos, E. (2004) *Raytheres*, a new name for *Raymondia* Campos, 2002 (Crustacea: Brachyura: Pinnotheridae) preoccupied by *Raymondia* Frauenfeld, 1855 (Hexapoda: Diptera: Streblidae). *Journal of Crustacean Biology*, 24, 372–372.
<http://dx.doi.org/10.1651/C-2443>
- Campos, E. (2006) Systematics of the genus *Scleroplax* Rathbun, 1893 (Crustacea: Brachyura: Pinnotheridae). *Zootaxa*, 1344, 33–41.
- Campos, E. (2007) Key to Pinnotheridae. In: Carlton, J.T. (Ed.), *The Light and Smith Manual. Intertidal Invertebrates from Central California to Oregon*. University of California Press, Berkeley, pp. 643–647.
- Campos, E. (2009) A new species and two new genera of pinnotherid crabs from the northeastern Pacific Ocean, with a reappraisal of the subfamily Pinnotherinae de Haan, 1833 (Crustacea: Brachyura: Pinnotheridae). *Zootaxa*, 2022, 29–44.
- Campos, E. (2013) Remarks on the sexual dimorphism and taxonomy of *Fabia* Dana, 1851 (Crustacea, Brachyura, Pinnotheridae). *Zootaxa*, 3616 (2), 190–200.
<http://dx.doi.org/10.11646/zootaxa.3616.2.7>
- Campos, E. & Campos, A.R. de (2012) The intertidal brachyuran crabs from estuaries of the west coast Baja California, Mexico (Crustacea: Brachyura). *Marine Biodiversity Records, Marine Biological Association of the United Kingdom*, 5 (e117), 1–7.
<http://dx.doi.org/10.1017/s1755267212000966>
- Campos, E., Campos, A.R. de & Ramirez, J. (1992) Remarks on distribution and hosts for symbiotic crustaceans of the Mexican Pacific (Decapoda and Isopoda). *Proceedings of the Biological Society of Washington*, 105, 753–759.
- Campos, E., Campos, A.R. de & Manriquez, I. (2009) Intertidal thalassinidean shrimps (Thalassinidea, Callinassidae and Upogebiidae) of the west coast of Baja California, Mexico: annotated checklist, key for identification, and symbionts. *Crustaceana*, 82, 1249–1263.
<http://dx.doi.org/10.1163/001121609X12481627024454>
- Campos, E., Díaz, V. & Gamboa-Contreras, J.A. (1998) Notes on distribution and taxonomy of five poorly known species of pinnotherid crabs from the eastern Pacific (Crustacea: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 111, 372–381.

- Campos, E., Félix-Pico, E.F. & García-Domínguez, F. (1995) Distribution and host for four symbiotic crustaceans of the Mexican Pacific (Stomatopoda and Decapoda). *Bulletin of the Southern California Academy of Sciences*, 94, 176–178.
- Campos, E. & Hernández-Ávila, I. (2010) Phylogeny of *Calyptraeothers* Campos, 1990 (Crustacea, Decapoda, Brachyura, Pinnotheridae) with the description of *C. pepeluusi* new species from the tropical Mexican Pacific. *Zootaxa*, 2691, 41–52.
- Campos, E. & Manning, R.B. (1998) *Pinnotheres malaguena* Garth, 1948, a new member of the genus *Fabia* Dana, 1851 (Crustacea: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 111, 912–915.
- Campos, E., Peláez-Zárate, V.A. & Solís-Marín, F.A. (2012) Rediscovery, hosts and systematics of *Holothuriophilus trapeziformis* Nauck, 1880 (Crustacea, Brachyura, Pinnotheridae). *Zootaxa*, 3528, 57–62.
- Campos, E. & Manning, R.B. (2000) The identities of *Pinnotheres nudus* Holmes, 1895 and *P. nudus* sensu Weymouth, 1910 (Crustacea: Decapoda: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 113, 799–805.
- Campos, E. & Vargas-Castillo, R. (2013) *Pinnotheres orcutti* Rathbun, 1918 a new member of the genus *Tumidothere* Campos, 1989 in the Eastern Tropical Pacific (Crustacea, Brachyura, Pinnotheridae). *Zootaxa*, 3666 (1), 84–92.
<http://dx.doi.org/10.11646/zootaxa.3666.1.8>
- Campos, E. & Vargas-Castillo, R. (2014) *Austinothere angelicus* (Lockington, 1877): the correct name for the symbiotic crab *Juxtafabia muliniarum* sensu Cabrera-Peña *et al.* (2001) (Crustacea, Brachyura, Pinnotheridae). *Latin American Journal of Aquatic Research*, 43, 598–603.
<http://dx.doi.org/10.3856/vol42-issue3-fulltext-17>
- Campos, E. & Wicksten, M.K. (1997) A new genus for the Central American crab *Pinnixa costaricana* Wicksten, 1982 (Crustacea: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 110, 69–73.
- Campos-González, E. (1986) Records and new hosts of pea crabs (Decapoda, Pinnotheridae) for Baja California, Mexico. *Veliger*, 29, 238–239.
- Campos-González, E. (1988) New molluscan hosts for two shrimps and two crabs of the coast of Baja California, with some remarks on distribution. *Veliger*, 30, 384–386.
- Campos-González, E. & Campoy-Favela, J.R. (1987) Morfología y distribución de dos cangrejos chícharo del Golfo de California (Crustacea: Pinnotheridae). *Revista de Biología Tropical*, 35, 221–225.
- Carlisle, J.G. Jr. (1969) Invertebrates taken in six year trawl study in Santa Monica Bay. *Veliger*, 29, 238–239.
- Castro, P. (2015) Symbiotic Brachyura, In: Castro, P., Davie, P., Guinot, D., Schram, F.R. & Vaupel Klein, J.C. von (Eds.), *Decapoda: Brachyura, Treatise on Zoology—Anatomy, Taxonomy, Biology. Vol. 9. Part C-I*. Brill, Leiden, pp. 543–581.
http://dx.doi.org/10.1163/9789004190832_012
- Christensen, A.M. & McDermott, J.J. (1958) Life-history and biology of the oyster crab, *Pinnotheres ostreum* Say. *Biological Bulletin*, 114, 146–179.
<http://dx.doi.org/10.2307/1538845>
- Davidson, E.S. (1968) The *Pinnotheres concharum* complex (Crustacea, Decapoda, family Pinnotheridae). *Bulletin of the Southern California Academy of Sciences*, 67, 85–88.
- Emparanza, E.J.M., Ulloa, R., Montiel-Ramos, A. & Molina-Ocampo, R. (2011) First record of the association of the crab *Pinnaxodes gigas* (Decapoda: Pinnotheridae) with the geoduck clam *Panopea globosa* (Bivalvia: Hiatellidae). *Marine Biodiversity Records, Marine Biological Association of the United Kingdom*, 4 (e40), 1–3.
<http://dx.doi.org/10.1017/s1755267211000352>
- Félix-Pico, E.F. (1992) Notas sobre la biología del cangrejo chícharo, *Tumidothere margarita* (Smith, 1869) (Decapoda: Brachyura: Pinnotheridae), en el sistema lagunar de Bahía Magdalena, Baja California Sur, México. *Proceedings of the San Diego Society of Natural History*, 25, 1–6.
- Garth, J.S. & Abbott, D.P. (1980) Brachyura: The True Crabs. In: Morris, R.H., Abbott, D.P. & Haderlie, E.C. (Eds.), *Intertidal Invertebrates of California*. Stanford University Press, Stanford, pp. 592–630.
- Glassell, S.A. (1933) Descriptions of five new species of Brachyura collected on the west coast of Mexico. *Transactions of the San Diego Society of Natural History*, 7, 331–344.
- Glassell, S.A. (1934) Affinities of the brachyuran fauna of the Gulf of California. *Journal of Washington Academy of Sciences*, 24, 296–302.
- Glassell, S.A. (1935a) New or little known crabs from the Pacific coast of northern Mexico. *Transactions of the San Diego Society of Natural History*, 8, 91–106.
- Glassell, S.A. (1935b) Three new species of *Pinnixa* from the Gulf of California. *Transactions of the San Diego Society of Natural History*, 8, 13–14.
- Glassell, S.A. (1938) New and obscure decapod Crustacea from the west American coasts. *Transactions of the San Diego Society of Natural History*, 8, 411–454.
- González-Peláez, S.S., Leyva-Valencia, I., Pérez-Valencia, S. & Lluch-Cota, D.B. (2013) Distribution limits of the geoduck clams *Panopea generosa* and *P. globosa* on the Pacific Coast of Mexico. *Malacologia*, 56, 85–94.
<http://dx.doi.org/10.4002/040.056.0206>
- Green, T.M. (1985) *Pinnotheres jamesi* synonymized with *P. reticulatus* (Decapoda: Brachyura). *Proceedings of the Biological Society of Washington*, 98, 611–614.
- Green, T.M. (1992) *Pinnaxodes gigas*, a new species of pinnotherid crab from the Gulf of California (Decapoda: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 105, 775–779.
- Griffith, H. (1987) Taxonomy of the genus *Dissodactylus* (Crustacea: Brachyura: Pinnotheridae) with descriptions of three new species. *Bulletin of Marine Science*, 40, 397–422.
- Hart, J.F.L. (1982) *Crabs and their Relatives of British Columbia*. British Columbia Provincial Museum. Handbook 40. British Columbia, Victoria, 267 pp.
- Hendrickx, M.E. (1990) Range extensions and host record for *Dissodactylus ususfructus* Griffith, 1987 (Crustacea: Brachyura:

- Pinnotheridae). *Proceedings of the Biological Society of Washington*, 103, 106–107.
- Hendrickx, M.E. (1995) Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 65, 125–150.
- Hendrickx, M.E., Brusca, R.C., Cordero, M. & Rodríguez-R, G. (2007) Marine and brackish-water molluscan biodiversity in the Gulf of California, Mexico. *Scientia Marina*, 71, 637–647.
<http://dx.doi.org/10.3989/scimar.2007.71n4637>
- Hernández-Ávila, I. & Campos, E. (2006) *Calyptraeothers hernandezi* (Crustacea: Brachyura: Pinnotheridae), a new crab symbiont of the West Indian cup-and-saucer *Crucibulum auricula* (Gmelin) (Mollusca: Gastropoda: Calyptraeidae) off Cubagua Island, Venezuela. *Proceedings of the Biological Society of Washington*, 119, 43–48.
[http://dx.doi.org/10.2988/0006-324X\(2006\)119\[43:CHCBPA\]2.0.CO;2](http://dx.doi.org/10.2988/0006-324X(2006)119[43:CHCBPA]2.0.CO;2)
- Holmes, S.J. (1895) Notes on west American Crustacea. *Proceedings of the California Academy of Sciences*, Series 2, 4, 563–588.
- Holmes, S.J. (1900) Synopsis of California stalk-eyed Crustacea. *Occasional Papers of the California Academy of Sciences*, 7, 1–262.
<http://dx.doi.org/10.5962/bhl.title.53705>
- Hopkins, T.S. & Scanland, T.B. (1964) The host relations of a pinnotherid crab, *Opisthopus transversus* Rathbun (Crustacea: Decapoda). *Bulletin of the Southern California Academy of Science*, 63, 175–180.
- Lemaitre, R. & Álvarez-León, R. (1992) Crustáceos decápodos del Pacífico Colombiano: lista de especies y consideraciones zoogeográficas. *Anales del Instituto de Investigaciones Marinas de Punta de Betín*, 21, 33–76.
- Manning, R.B. & Felder, D.L. (1989) The *Pinnixa cristata* complex in the western Atlantic, with descriptions of two new species (Crustacea: Decapoda: Pinnotheridae). *Smithsonian Contributions to Zoology*, 473, 1–26.
<http://dx.doi.org/10.5479/si.00810282.473>
- Palacios-Theil, E., Cuesta, J.A. & Felder, D.L. (2016) Molecular evidence for non-monophyly of the pinnotheroid crabs (Crustacea: Brachyura: Pinnotheroidea), warranting taxonomic reappraisal. *Invertebrate Systematics*, 30, 1–27.
<http://dx.doi.org/10.1071/IS15023>
- Paredes-Ríos, G.A. & Balart, E.F. (1999) Corroboration of the Bivalve, *Pinna rugosa*, as a host of the Pacific pearlfish, *Encheliophis dubius* (Ophidiiformes: Carapidae), in the Gulf of California, Mexico. *Copeia*, 1999, 521–522.
<http://dx.doi.org/10.2307/1447503>
- Pearce, J.B. (1966) The biology of the mussel crab, *Fabia subquadrata*, from the waters of the San. Juan archipelago, Washington. *Pacific Science*, 20, 3–35.
- Pearse, J.B. (1969) On reproduction in *Pinnotheres maculatus* (Decapoda: Pinnotheridae). *Biological Bulletin*, 127, 384.
- Pohle, G.W. & Marques, F. (1995) First zoea of *Dissodactylus glasselli* Rioja and new range and host records for species of *Dissodactylus* (Brachyura: Pinnotheridae), with a discussion of host-symbiont biogeography. *Proceedings of the Biological Society of Washington*, 108, 247–256.
- Rathbun, M.J. (1918) The grapsoid crabs of America. *Bulletin of the United States National Museum*, 97, 1–461.
- Rathbun, M.J. (1923) Scientific results of the expedition to the Gulf of California in charge of C.H. Townsend, by the U.S. Fisheries steamship ‘Albatross,’ in 1911. Commander G.H. Burrage, U.S.N., Commanding XIII. The brachyuran crabs collected by the U.S. Fisheries steamer ‘Albatross’ in 1911, chiefly on the west coast of Mexico. *Bulletin of the American Museum of Natural History*, 48, 619–637.
- Ricketts, E., Calvin, J., Hedgepeth, J. & Phillips, W. (1985) *Between Pacific Tides*. Stanford University Press, Stanford, 652 pp.
- Salgado-Barragán, J. (2015) A new species of *Pinnixa* (Crustacea: Brachyura: Pinnotheridae) from Mazatlan, Sinaloa, Mexico. *Revista Mexicana de Biodiversidad*, 86, 629–633.
<http://dx.doi.org/10.1016/j.rmb.2015.03.001>
- Scanland, T.B. & Hopkins, T.S. (1978) A supplementary description of *Pinnixa tomentosa* and comparison with the geographically adjacent *Pinnixa tubicola* (Brachyura, Pinnotheridae). *Proceedings of the Biological Society of Washington*, 91, 636–641.
- Schmitt, W.L. (1921) The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer “Albatross” in connection with the biological survey of San Francisco Bay during the years 1912–1913. *University of California Publications in Zoology*, 23, 1–470.
- Schmitt, W.L., McCain, J.C. & Davidson, E.S. (1973) Fam. Pinnotheridae, Brachyura I: Decapoda I. In: Gruner, H.-E. & Holthuis, L.B. (Eds.), *Crustaceorum Catalogus*. W. Junk, Den Haag, 3, pp. 1–160.
- Vargas-Castillo, R. & Wehrmann, I.S. (2009) Decapod Crustaceans, In: Wehrmann, I.S. & Cortés, J. (Eds.), *Marine Biodiversity of Costa Rica, Central America*. Springer Verlag, Berlin, pp. 1–538.
http://dx.doi.org/10.1007/978-1-4020-8278-8_19
- Wang, C. & Fiedler, P.C. (2006) ENSO variability and the eastern tropical Pacific: a review. *Progress in Oceanography*, 69, 239–266.
<http://dx.doi.org/10.1016/j.pocean.2006.03.004>
- Wicksten, M.K. (1983) A monograph on the shallow water caridean shrimps of the Gulf of California, Mexico. *Allan Hancock Monographs in Marine Biology*, 13, 1–59.
- Wicksten, M.K. (1989) A key to the palaemonid shrimp of the Eastern Pacific region. *Bulletin of the Southern California Academy of Sciences*, 88, 11–20.
- Wicksten, M.K. (2012) Decapod Crustacea of the Californian and Oregonian zoogeographic provinces. *Zootaxa*, 3371, 1–307.
- Zmarzly, D.L. (1992) Taxonomic review of pea crabs in the genus *Pinnixa* (Decapoda: Brachyura: Pinnotheridae) occurring on the California shelf, with descriptions of two new species. *Journal of Crustacean Biology*, 12, 677–713.